Phylogeny of the Lizard Subfamily Lygosominae (Reptilia: Scincidae), with Special Reference to the Origin of the New World Taxa

Masanao Honda¹*, Hidetoshi Ota², Gunther Köhler³, Ivan Ineich⁴, Laurent Chirio⁴, Szu-Lung Chen⁵ and Tsutomu Hikida⁶

¹School of Allied Medical Sciences, Shinshu University, Asahi, Matsumoto, Nagano 390-8621, Japan
²Tropical Biosphere Research Center, University of the Ryukus, Nishihara, Okinawa 903-0213, Japan
³Forschungsinstitut und Naturmuseum Senckenberg, Senckenberganlage 25, Frankfurt am Main D60325, Germany
⁴Muséum national d’Histoire naturelle, 25 rue Cuvier, F-75005 Paris, France
⁵Taipei Zoo, 30 Xin Kuang Road, Sec 2 Mu Zha Wen Shan Taipei 116, Taiwan, R.O.C.
⁶Department of Zoology, Graduate School of Science, Kyoto University, Sakyo, Kyoto 606-8502, Japan

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Phylogenetic relationships of the three lygosomine skink genera occurring both in the Old World and the New World (Mabuya, Scincella and Sphenomorphus) were inferred from mitochondrial DNA sequence of 12S and 16S rRNA genes. Results strongly suggested the non-monophyly for any of these three genera. Within the Mabuya group, Asian members appear to have diverged first, leaving the Neotropical and the Afro-Malagasy Mabuya as sister groups. These relationships, together with the absence of extant or fossil representatives of the Mabuya group from North America, strongly suggest the trans-Atlantic dispersals of Mabuya from Africa to Neotropics. Our results also indicated a closer affinity of the New World Scincella with the New World Sphenomorphus than with the Old World Scincella. Such relationships suggest the trans-Beringian dispersal of the common ancestor from Asia and its subsequent divergence into the North American Scincella and the Neotropical Sphenomorphus.

Key words: biogeography, Lygosominae, Mabuya, Scincella, Sphenomorphus

INTRODUCTION

Taxonomic composition of herpetofauna in the New World region is known to remarkably differ from that in the Old World. This leads systematists and biogeographers to vigorous debates regarding the historical and environmental factors responsible for the emergence of current diversity in the New World reptiles and amphibians (e.g., Duellman, 1979). Especially, process of evolution and range extension in lineages common to both worlds has been one of the major subjects of such debates, e.g., Gondwanaland origin vs Laurasian origin, and current diversity as a consequence of multiple colonizations vs in situ radiation.

Formerly, hypothetical scenarios, chiefly invoking vicariance as involved by the break-up of old super-continents and their derivatives, were usually proposed to explain distributions and phylogenetic patterns of reptiles, amphibians and various other organisms shared by the New World and other old land masses (e.g., see Duellman [1979], Presch [1983], and Estes and Pregill [1988] for review). It has recently been re-emphasized, however, that some of those organisms, lizards in particular, often disperse overseas by rafting (Censky et al., 1998), sometimes for such a long distance as being comparable to those across large oceans (e.g., Gibbons, 1985; Raxworthy et al., 2002). Obviously, this issue has made it more difficult to choose the most plausible hypothesis over the others for the distribution and origin of current diversity of each taxon common to the New World and other regions. Recent progresses in the theory of molecular evolution and methods of molecular phylogenetics can offer a much effective tool for solutions of such problems, because they together can provide a highly reliable framework for the estimation of relative and absolute timing of divergence in a lineage in problem (e.g., Mindell and Thacker, 1996).
The Scincidae is the largest family of extant lizards and consists of four subfamilies: Scincinae, Acontinae, Feyliniinae and Lygosominae (Greer, 1970a). Of these, the Lygosominae contains 45 genera and over 600 species (Matsui, 1992) distributed mainly from temperate to tropical areas of the Old World (East, Southeast and South Asia, Australasia, sub-Saharan Africa, and Indian Ocean islands including Madagascar), but also in some areas of the New World. In the latter, only three genera (Mabuya, Sphenomorphus and Scincella: Fig. 1), all common to the Old World, occur for this subfamily (Greer, 1970a; Matsui, 1992; Zug, 1993).

Of these three genera, Scincella is confined to the area from eastern North America down to Mexico within the New World, and is considered to have reached there by trans-Beringian dispersals (Fig. 1), because this genus is much more diversified in Asia including the Far East (Tihen, 1964; Greer, 1974; Ouboter, 1986; Chen et al., 2001). Origin of the New World Mabuya and Sphenomorphus, both confined to the Neotropical region (Greer, 1970a, 1974; Myers and Donnelly, 1991), are more puzzling because they are much more isolated from the Old World congeners by broad intervening geographical gaps. With respect to the Neotropical Mabuya, Greer (1977), on the basis of morphological analyses, assumed its relatively recent derivation from African radiation by trans-Atlantic dispersals (Fig. 1). Mausfeld et al. (2000) depicted relationships of Mabuya on the basis of analysis of sequence variations in a part of the mitochondrial 16S ribosomal RNA (rRNA) gene, in which the one Neotropical representative examined by them (M. cf. bistriata) was located basal to all Afro-Malagasy congeners examined. However, such a relationships failed to receive a substantial bootstrap support (≥ 70%), and, probably because of this, those authors did not make any discussion relevant to the origin of the Neotropical species. On the other hand, no hypotheses have been formulated regarding the origin and relationships of the Neotropical Sphenomorphus. Considering the fact that all Old world congeners are confined to East and Southeast Asia including the Indo-Australian Archipelago (Matsui, 1992; Cogger, 2000) and that putative close relatives of the genus (Calyptotis, Ctenotus, Cyclodina, Eulamprus and Glaphyromorphus: e.g., Greer, 1979b; Cogger, 1983) occur exclusively in Australasia (Cogger, 2000), migration of the ancestor of the Neotropical Sphenomorphus via trans-Pacific dispersals might be likely (Fig. 1).

Recently we analyzed sequence variations in mitochondrial 12S and 16S rRNA genes for the Old World lygosomines phylogenetically. Results of the analyses, while recognizing five distinct lineages within the subfamily (i.e., Sphenomorphus, Lygosoma, Egernia, Eugongylus and Mabuya groups), revealed non-monophyly for the genus Mabuya, as well as for the genus Sphenomorphus (Honda et al., 2000). Results also indicated frequent occurrences of homoplasy in morphological characters in the subfamily. These findings also support the necessity of molecular phylogenetic approaches to problems relevant to the origin of the New World lygosomine taxa, because their generic assignments have been made almost solely on morphological grounds (e.g., Greer, 1970a, 1979b; but see Mausfeld et al., 2000)

In this study, we sequenced mitochondrial DNA for representatives of all three New World lygosomine genera, and analyzed resultant data together with corresponding data previously published (Honda et al., 2000) or newly

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Fig. 1. A map showing distributions of Mabuya, Scincella and Sphenomorphus, and their entry ways to the New World postulated in the previous and present studies. Open, stippled and hatched areas represent approximate ranges of Mabuya, Scincella and Sphenomorphus, respectively.
obtained for their Old World “congeners” and other lygosomines and scincines. Our purposes are to establish a reliable phylogenetic hypothesis for the New World lygosomine skinks, and to infer the historical biogeographical processes of their emergences accordingly.

**MATERIALS AND METHODS**

**Samples analyzed.** Two species of the Neotropical *Mabuya* (*M. nigropunctata* and *M. unimarginata*), one

<table>
<thead>
<tr>
<th>Sample Group</th>
<th>Locality</th>
<th>Accession numbers</th>
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<tr>
<td>M. nigropunctata</td>
<td>French Guiana</td>
<td>AB057384*, AB057399*</td>
</tr>
<tr>
<td>M. unimarginata</td>
<td>Honduras</td>
<td>AB057387*, AB057398*</td>
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* Examined in the present study. See Appendix for detailed localities.
species of the Neotropical *Sphenomorphus* (*S. cherriei*), and the one North American *Scincella* (*S. lateralis*) were examined. Samples representing eight species of the Old World *Mabuya*, one Asian *Scincella* (*S. rupicola*), one Australian *Tiliqua*, and one *Scincus* (belonging to the Scincinae) were also subjected to the sequencing procedure (Table 1, see Appendix for further details). Furthermore, we incorporated into the analyses data for other skinks representing the five major lineages of the subfamily Lygosominae, and the subfamily Scincinae published in our previous study (Honda et al., 1999b,c, 2000; Table 1). Of these, *Eumeces latiscutatus*, *E. schneiderii* and *Scincus scincus* were regarded as outgroups, because the subfamily Scincinae, to which those species belong, is considered to be basal to the Lygosominae (Greer, 1970a).

**Extraction, amplification and sequencing of DNA.** The methods of DNA extraction, amplification and sequencing are described in detail elsewhere (Honda et al., 1999a,b). Previous studies revealed a relatively large degree of genetic divergences among lygosomite skinks (e.g., Honda et al., 2000; Mausfeld et al., 2000). Thus, we used 12S and 16S rRNA genes to avoid saturation of base substitutions because these domains seem to evolve more slowly than other mitochondrial genes (e.g., Keogh, 1998; Lee, 2000).

A part [approximately 1,250 base pairs (bp)] of mitochondrial 12S and 16S rRNA genes were amplified using the polymerase chain reaction (PCR) using primers: L1091 (5'-AAACTGGGATTAGATACCCACTAT-3') and H1478 (5'-GAGGCTGCAGGGGCGGTTGTGT-3') (Kocher et al., 1989) for 12S rRNA, and L2206 (5'-GGGCTAAAAGACGACGGT-3'), H3056 (5'-CTCCTGGTCAGAGATCCGTTAGG-3') (Hedges et al., 1993) and H2741 (5'-AAGCTTCCAGGGTCTTCTGCT-3') (Honda et al., 2000) for 16S rRNA. The DNA sequences have been submitted to the DDBJ database, and their accession numbers are given in Table 1.

**Phylogenetic analyses.** Alignments for DNA sequences were determined based on maximum nucleotide similarity using CLUSTAL X 1.8 (Thompson et al., 1994). In the previous study (Honda et al., 2000), we adjusted the output from CLUSTAL X with default gap penalties by eye considering the possible presence of secondary structures in the rRNA genes. However, secondary structures assumed as a result of this treatment were rather unstable because of the lack of comparable information for closely related taxa, and topologies of resultant trees were virtually identical between this procedure and those using the aligner. Thus, we henceforth refer only to phylogenetic analyses using sequence data that were aligned simply on the basis of the maximum similarity criterion, excluding insertions and deletions. We believe that this designation should not have given any sources of substantial errors to subsequent considerations.

The neighbor-joining (NJ) method (Saitou and Nei, 1987) was applied to infer relationships among taxa on the basis of a pairwise matrix of the distance from Kimura’s (1980) two-parameter model, using CLUSTAL X 1.8 (Thompson et al., 1994). The maximum-likelihood (ML, empirical base frequencies and equal rate substitution model) and maximum-parsimony (MP, no bias between transition and transversion) analyses were also conducted using heuristic search option of PAUP* 4.0b (Swofford, 1998). In these three analyses, confidences were assessed by bootstrap resamplings (Felsenstein, 1985). In ML, validity of each branch, as expressed by its length, was also tested statistically by use of PHYLIP 3.6a (Felsenstein, 1993).

The interpretation of bootstrap proportions (BPs) in the context of validity of corresponding nodes is still a matter of serious debates (see Felsenstein and Kishino [1993], and Hillis and Bull [1998], for example). We tentatively followed Shaffer et al. (1997), and considered BP ≥ 90% as highly significant, 90% > BP ≥ 70% as marginally significant, and 70% > BP ≥ 50% as constituting limited evidence of monophyly.

**Inference of dates of divergence.** According to the theory of molecular clocks, the degree of mitochondrial DNA substitutions between taxa can be used to date evolutionary divergences. We adopted rates of 2% (e.g., Brown et al., 1982) and 0.65% nucleotide substitutions per million years (MY) (Bermingham et al., 1997; Macey et al., 1998a,b, 1999; Schulte et al., 2000) to infer dates of divergences between the Old World and New World taxa.

**RESULTS**

**Nucleotide substitutions and estimated dates of divergences.** The amplified fragment of the 12S rRNA gene consisted of 397 total sites, 220 of which were variable. For the 16S rRNA fragment, there were 856 total aligned sites, of which 446 were variable. Intergeneric nucleotide replacements within the Lygosominae varied from 105 bp (*Corucia vs Egerinia*) to 251 bp (*Sphenomorphus cherriei vs Eugongyulus*). Intra-generic nucleotide replacements involved 85–208 bp, 146 bp and 138–213 bp in *Mabuya*, *Scincella* and *Sphenomorphus*, respectively.

The mean number of substitutions between African and American *Mabuya* subgroups, which showed sister-relationships with each other (see below), was 13.6%, whereas that between the Asian *Scincella* and its sister group in the New World (*New World Sphenomorphus* and *Scincella*: see below) was 13.4%. These values are interpreted to reflect divergence times of 6.8–20.9 MY and 6.7–20.6
Origin of New World lygosomine skinks

Fig. 2. Phylogenetic relationships of the subfamily Lygosominae derived from 12S and 16S rRNA sequence data. Names in bolds indicate New World taxa. (A) Neighbor-joining (NJ) dendrogram. Numbers beneath branches are BPs at least 50% of the 1,000 bootstrap replications. Nodes with bold numbers indicate relationships referred to in the text. Bar equals 0.1 unit of Kimura’s two-parameter distance. (B) Maximum-likelihood (ML) dendrogram (ln likelihood = –21052.3). All branches were statistically significant (P < 0.01). Bar equals 0.1 unit. Bold numbers above branches are identical with those in NJ and MP dendrograms. Branches without BP values were not supported in ≥ 50% of the 1,000 replicates. (C) Maximum parsimony (MP) dendrogram using heuristic option (3,897 steps, 545 bp informative under the condition of parsimony, consistency index = 0.310, homoplasy index = 0.690, retention index = 0.409). Bar equals 10 bp replacements. Branches without BP values were not supported in ≥ 50% of the 1,000 replicates.
Phylogenetic relationships. The NJ dendrogram derived from aligned sequences is shown in Fig. 2A. The monophyly of the Lygosominae was supported in 62% BP (node 1). Within the Lygosominae, five distinct clusters (nodes 2, 4–7), corresponding to the five infrasubfamilial lineages recognized in our previous study (Honda et al., 2000), were supported with much higher BPs (= 90) with a primary dichotomy being located between the Sphenomorphus group (node 2: 94%) and the non-Sphenomorphus assemblage (node 3: 93%). The non-Sphenomorphus assemblage was divided into the Egerinia (node 4: 100%), Lygosoma group (node 5: 100%), and the remainder (75%), and the latter further into the Scincella group (node 6: 100%) and the Mabuya group (node 7: 90%).

The New World Sphenomorphus (Sph. cherriei) and Scincella (Sc. lateralis) constituted a monophyletic group with a relatively high BP (84%) in the Sphenomorphus group, and the sister-group relationship of the New World Sphenomorphus—Scincella cluster with the Old World Scincella (Sc. rupicola) received a lower but substantial BP support (node 12: 70%). Three Asian Sphenomorphus incorporated into the analysis (Sph. praesignis, Sph. indicus and Sph. maculatus), while failing to constitute a monophyletic group by themselves as reported previously (Honda et al., 2000), were rather distantly located to the New World Sphenomorphus—Scincella cluster within the Sphenomorphus group (Fig. 2A).

The Mabuya group, on the other hand, was split into two well supported clusters, of which one consisted of the Asian Mabuya and the two arboreal genera, Apterygodon and Dasia (node 8: 98%: henceforth referred to as the Asian Mabuya subgroup), whereas the other of the American, African and Malagasy members of Mabuya (node 9: 95%). The latter was further split into the Afro-Malagasy Mabuya (node 10: 93%, African Mabuya subgroup) and Neotropical Mabuya (node 11: 100%, American Mabuya subgroup).

Results of ML (Fig. 2B) and MP analyses (Fig. 2C) are consistent with the NJ dendrogram in terms of the existence of nodes 1–12, and monophyly of the New World Scincella and the New World Sphenomorphus.

DISCUSSION
Diversification and the Old World—New World dispersals of lygosomines inferred from molecular data. Within the subfamily Lygosominae, three evolutionary lineages (i.e., Eugongylus, Sphenomorphus, and Mabuya groups sensu lato) had been originally recognized on the basis of morphological and karyological data (King, 1973, 1990; Greer, 1979b, 1989; Hardy, 1979; Baverstock and Donnellan, 1990; Donnellan, 1991a,b; Ota et al., 1988, 1991, 1995, 1996; but see Hutchinson, 1981). However, based on the DNA sequence data, Honda et al. (1999b,c, 2000) negated such a view, and recognized five distinct clades within the subfamily by splitting the Mabuya group sensu lato into the Egerinia, Lygosoma and Mabuya groups (Honda et al., 2000). Results of the present analyses by incorporating data for New World and additional Old World taxa support such a view, and confirm allocations of the New World Sphenomorphus and Scincella to the Sphenomorphus group, and the New World Mabuya to the Mabuya group (sensu Honda et al., 2000).

Some authors proposed an explanation for the current phylogeographical patterns in lizards on the ground of vicariance as involved by major plate tectonic events (e.g., Estes, 1983), whereas others invoked dispersals between continents after formations of Atlantic and Pacific Oceans rather than vicariances through the continental drift (e.g., Presch, 1988). Recent molecular studies demonstrated that both vicariance (e.g., in the iguanians: Macey et al., 1997) and dispersals (e.g., in the varanids: Fuller et al., 1998) have played a substantial role for the foundation of current diversity and distribution of lizards.

Phylogenetic relationships in the present study indicate that divergences of the Old World and New World lygosomines took place later than those of the five evolutionary lineages. The separation of African and South American landmasses within the Gondwanaland is considered to have completed approximately 100 MY (Smith et al., 1994; Plate Project, 1998), a period prior to the evolution of the lygosomine skinks as suggested by fossil evidence (Estes, 1983). Moreover, gross estimations of dates of the Old World—New World divergences by us never exceed this value (see above). These strongly suggest dispersals between the Old World and the New World by relevant lygosomine lineages after the formations of Atlantic and Pacific Oceans like a few other groups of lizards (e.g., Hemidactylus brookii and H. mabuia: Kluge, 1969).

Origin and evolution of the New World Mabuya. Several previous authors assumed that the present Neotropical Mabuya had originated from the trans-Atlantic dispersals from Africa (Greer, 1970a, 1977; Laurent, 1979), because they more closely resemble some African Mabuya than the Asian congeners. All Southeast Asian species, for example, have pterygoid teeth, whereas these teeth have been lost in all Neotropical species and about a half of the African species (Greer, 1970b). Present results, indicating a sister relationship between the Afro-Malagasy (African Mabuya subgroup) and Neotropical Mabuya (American Mabuya subgroup), together with the absence of extant or fossil Mabuya or its close relatives in Australia and North America (Greer, 1979b; Estes, 1983; Honda et al., 2000), strongly support the above view for
the origin of Neotropical Mabuya. Distribution of Mabuya in Madagascar is supposed as a consequence of more recent secondary dispersals from Africa.

Dunn (1936) surmised a close affinity of the Neotropical mainland and Caribbean Island species with the African *M. affinis* group. Furthermore, very low species diversity in the Neotropical Mabuya as compared to the African Mabuya is often interpreted as reflecting a relatively short history of the former (see Greer, 1970a for further discussion). These imply that the colonization of Mabuya into the Neotropical region occurred subsequent to the major radiation of the genus in Africa. However, present results, showing a basal dichotomy of the Neotropical and Afro-Malagasy clusters prior to an extensive diversification in the latter, do not support such a view, or close affinity of the Neotropical Mabuya with African *M. affinis* (contra Dunn, 1936). The low species diversity of the Neotropical Mabuya may actually be a consequence of occupancy of otherwise available niches by micro-teiids or even polychrotids, which had radiated within South and central America prior to the arrival of Mabuya, producing a number of skink-like forms (e.g., *Cnemidophorus* and *Tretioscincus*: Greer, 1970a).

Greer and Nussbaum (2000) argued that the African and American Mabuya have a primitive state in the overlap pattern between the parietal and the upper anterior temporal scales (parietal overlapping the upper anterior temporal), whereas most of the Asian species and all endemic Madagascan species of the genus possess a derived state (the upper anterior temporal overlapping the parietal). Present results suggest that the latter state independently evolved in the common ancestor of the Asian Mabuya and in the lineage leading to the Malagasy congeners.

Some authors predicted the possible non-monophyly of the genus Mabuya due to its wide distribution and great morphological diversity (e.g., Greer, 1977). Based on molecular data, Honda et al. (1999b) argued for the non-monophyly even within the Old World members. On the other hand, Greer and Broadley (2000) surmised monophyly of Mabuya by demonstrating one diagnostic character of the genus (the reduction in the contact between the first supraocular and frontal, but exclusive of five species). Present results confirm our previous conclusion (Honda et al., 2000), because they clearly indicate a close affinity of the Asian Mabuya with the two arboreal genera, *Apterygodon* and *Dasia*, rather than with the non-Asian congeners. Because the type species of the genus Mabuya is *M. mabouya* from the Neotropical region (Fitzinger, 1826), reassignment of the Asian species to a different genus would be needed when the above relationships are verified by the analyses with the remaining species of this genus.

**Origin and evolution of the New World Scincella and Sphenomorphus.** As is mentioned above, Scincella had been considered to have reached the New World by the trans-Beringian dispersal from Asia (e.g., Tihen, 1964; Greer, 1974). With respect to the Neotropical Sphenomorphus, no concrete hypotheses have ever been formulated regarding their relationships or origins. Present results clearly indicate a distant affinity of the Neotropical Sphenomorphus from Asian “congeners”, confirming the residual, non-monophyletic nature of the genus (e.g., Greer, 1979a; Brown and Alcala, 1980; Honda et al., 2000). From our results, it is possible that the Neotropical Sphenomorphus is actually a sister group of the New World Scincella, and that they altogether constitute a sister group to the Old World Scincella. Such relationships suggest that the ancestor of the Neotropical Sphenomorphus first reached the New World by trans-Beringian dispersals as a common ancestor with the New World Scincella. The ancestor may then have extended its distribution down to the central America and diversified there into the Neotropical “Sphenomorphus” subsequently.

Smith and Taylor (1950) listed cherriei and its relatives as Scincella. Greer (1974) tentatively reassigned these species to the genus Sphenomorphus, because Sph. cherriei, which was assumed to be most primitive in the Neotropical assemblage, had a few character states (scaly lower eyelids and a postorbital bone) common to the Old World Sphenomorphus but not to the North American Scincella. Subsequent authors followed this arrangement and referred to cherriei and its Neotropical relatives as Sphenomorphus (e.g., Myers and Donnelly, 1991). However, our results, as well as the possession of the postorbital bone by most Asian Scincella (Greer, 1974), suggest that the presence of this bone element is actually a plesiomorphic state in the whole Scincella—Neotropical Sphenomorphus lineage, and that Sc. lateralis has lost it secondarily after the divergence from the New World “Sphenomorphus”.

In a few lizard groups including the Lygosominae, the scaly eyelid is considered to be a primitive state, from which the more advanced windowed eyelid has evolved as an adaptation to xeric environments (e.g., Greer, 1983, 1989). However, since both the Old World Scincella and the North American Sc. lateralis have windowed eyelids, the scaly eyelid of Sph. cherriei may represent a case of reversely directed evolution of this character in a highly humid tropical rain forest (Myers and Donnelly, 1991). Based on the present results, we suggest reassignments of Sph. cherriei and its Neotropical relatives to the genus Scincella. Further studies with additional materials for other Neotropical species (Smith and Taylor, 1950; Greer, 1974; Myers and Donnelly, 1991) are desired to verify this account.
Prof. H. M. Smith pulled our initial attention to the problems discussed here. We are much indebted to him also for his kind provision of pertinent literature. Also, we would like to thank M. Matsui, K. Araya, M. Toda, S. Panha, J. Nabhitabhata and T. Chan-Ard for providing us with various help and encouragement during our field sampling, to N. Nikoh for help with phylogenetic analyses, and to G. M. Burghardt, A. Mori and J. C. de Massary for the arrangement to obtain a few crucial materials. Special thanks are due N. Satoh and members of his laboratory for continuous support for our laboratory experiments. Experiments were also carried out using the facility of the Kyoto University Museum through the courtesy of T. Nakabo and M. Motokawa. Honda, Ota and Hikida are especially grateful to M. Matsui, and Hikida also to S. Yamagishi for providing opportunities to visit Thailand and Madagascar, respectively. Our research was partially supported by Grants-in-Aid from the Japan Ministry of Education, Science, Sports and Culture (Overseas Researches Nos. 04041068, 06041066 and 18041144 to Matsui; 06041093 and 11691183 to Yamagishi), and the Nakayama Foundation for Human Science (to Honda).

REFERENCES


Appendix.

Localities and catalogue numbers of voucher specimens. The specimens were deposited in the herpetological collection of Department of Zoology, Kyoto University (KUZ), Muséum national d'Histoire naturelle (MNHN) and Senckenberg Museum of Frankfurt am Main (SMF). Those listed in Honda et al. (2000) are omitted except for KUZ 46926. This specimen was listed as Tiliqua gigas in Honda et al. (1999b, 2000), because of its similarity with $T. \text{gigas}$ in scalation. However, its coloration is different from that of typical $T. \text{gigas}$, and is closer to that of $T. \text{scincoides}$ sensu lato (i.e., including $T. \text{gigas}$). Other characters, including scalations are also within ranges of variations in the latter species. We thus tentatively re-assign this specimen to $T. \text{scincoides}$. An asterisk (*) indicates that a specimen was imported by a pet dealer and that its locality is thus unknown.